FOG-Aleut-10F Rec'd 5/24/2005

Estimating movement and abundance of Atka mackerel (*Pleurogrammus monopterygius*) with tag-release-recapture data

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Running Title: Atka mackerel mark-recapture experiment

ABSTRACT

A mark-recapture experiment was conducted in Seguam Pass, Alaska, to estimate local Atka mackerel *(Pleurogrammus monopterygius*) abundance and to evaluate the efficacy of trawl exclusion zones around Steller sea lion (*Eumetopias jubatus*) rookeries. Atka mackerel were found in dense aggregations near the Aleutian Islands where they are a major prey item of endangered Steller sea lions. In 1999, 1375 tagged fish were released and a biomass of 76,679 metric tons (t) was estimated outside a trawl exclusion zone using a simple Peterson model. In 2000, 8773 tagged fish were released and the estimated biomasses were 117,900 t inside and 82,057 t outside the trawl exclusion zones using an integrated tagging model. Movement into the open zone was small after 107 days (0.6%), whereas movement from the open area was potentially large but highly uncertain after 107 days (81%). Our model suggests that trawl exclusion zones in Seguam Pass are effective in separating a large biomass of potential prey for Steller sea lions from the immediate effects of local fisheries. Atka mackerel do not appear to move substantially outside their local aggregations (< 70 km) and they show strong habitat preferences within their local home ranges. In one instance, fish released in an area of low Atka mackerel abundance returned to their capture location about 2 miles away. Thus individual Atka mackerel may have an affinity for particular areas within their home range, perhaps resulting from adaptations to local oceanic conditions along the Aleutian Island archipelago.

Keywords: Aleutian Islands, Atka mackerel, ecosystem, movement rate, population abundance, tag release-recapture, trawl-exclusion zone

INTRODUCTION

Atka mackerel (*Pleurogrammus monopterygius*) is a major prey species of Steller sea lions (*Eumetopias jubatus*) in the Aleutian Islands area as well as an important commercial species targeted by the U.S. groundfish fishery (NMFS, 1995; Sinclair and Zeppelin, 2002). The listing of the western stock of Steller sea lions as endangered under the Endangered Species Act (ESA; Fritz *et al.*, 1995) in 1990 prompted the need to accurately estimate Atka mackerel abundance on small spatial and temporal scales. The Atka mackerel fishery occurs in federal waters and Section 7 of the ESA mandates that federal actions such as this fishery will not jeopardize the continued existence of Steller sea lions, nor adversely modify its designated critical habitat (e.g., reduce prey abundance; Fritz *et al.,* 1995). Critical habitat of Steller sea lions was defined as habitat being essential to the conservation of the species (Fritz *et al.,* 1995).

One hypothesis for the decline and lack of recovery of the western stock of Steller sea lions is competition for prey with fisheries (Loughlin, 1987; NAS, 1996). Historically, the Atka mackerel fishery has operated close to sea lion rookeries in the Aleutian Islands, and largely within sea lion critical habitat. In addition, scientists have speculated that commercial fisheries for Atka mackerel may cause localized prey depletions for Steller sea lions (Lowe and Fritz, 1997). To reduce the likelihood that fisheries would cause localized prey depletions around sea lion rookeries, the North Pacific Fishery Management Council (NPFMC) and the National Marine Fisheries Service (NMFS) took a series of steps to protect critical habitat (Fritz *et al.*, 1995; Fritz and Ferrero, 1998). One measure established Atka mackerel trawl exclusion zones around sea lion rookeries in an effort to maintain prey population densities in important foraging areas, particularly for female sea lions with pups. However, when rookery trawl exclusion zones were implemented in 1992, it was not known if they would be effective in protecting Atka mackerel abundance on scales appropriate to foraging sea lions, namely 0-20 nautical miles (n mi) from terrestrial rookeries. To determine the efficacy of the no-trawl zones, it is necessary to estimate Atka mackerel abundance on small spatial scales, as well as their movement between areas open and closed to the fishery.

Atka mackerel abundance in the Aleutian Islands has been assessed by bottom trawl surveys using a random, area-depth stratified design (Britt and Martin, 2001; Zenger, 2002). Survey biomass estimates of Atka mackerel for the entire Aleutian Islands region are associated with high variability; coefficients of variation (CVs) of estimates from eight surveys conducted between 1980 and 2002 ranged between 0.15 and 0.33, with five CVs > 0.28 across the entire survey data set (Lowe *et al.*, 2003). On smaller spatial scales (NMFS management area, e.g., approximately one-third of the Aleutian Islands region) the CVs from these surveys have been even larger, ranging from 0.18 to 0.83 (Lowe *et al.*, 2003).

Estimating the abundance of patchily distributed fishes and crustaceans using trawls is problematic due to highly skewed distributions and large variances of the data (Kappenman, 1999). Alternative methods include acoustic technologies (Gunderson, 1993) and mark-recapture methods (Peterson, 1896; Seber, 1982). Atka mackerel do not possess a swim bladder and are therefore difficult to detect acoustically.

Unlike trawl surveys, variance estimates from mark recapture studies are unaffected by patchiness (assuming random mixing for marked and unmarked fish). Further, in a fished population, the industry can be part of the tag recovery process, thus reducing charter costs that can be substantial in remote regions such as the Aleutian

Islands. However, involvement of the fishing industry requires estimation of a tag reporting rate to avert biased estimates.

A pilot study was conducted in August 1999 to examine the feasibility of tagging Atka mackerel to obtain preliminary estimates of tag loss (through double tagging) and tag-related mortality (by holding tagged and untagged fish in running seawater tanks for 12 days). This study revealed that initial tag-related mortality was low (< 2%), and that tagging large numbers of fish in charters of 2-3 weeks duration was affordable. Consequently, in August 2000 a large-scale tagging experiment was conducted to obtain estimates of Atka mackerel population abundance and movement between fished and unfished areas. This paper summarizes the results of the 1999 and 2000 experiments, including estimation of tag reporting rates, initial mortality due to tagging, and tag loss. Only biomass was estimated from the results obtained in 1999 (Peterson, 1896). In 2000, however, both movement between areas open and closed to the fishery and biomass in both areas were estimated using an integrated movement and biomass model developed here, but built on the previous work of Hilborn (1990).

Study population

In the Aleutian Islands Atka mackerel are generally aggregated in dense patches in areas of strong currents such as island passes. They comprise the largest fraction of the groundfish biomass in the Aleutian Islands region (Zenger, 2004) with an estimated exploitable biomass of 358,303 metric tons (t) (Lowe *et al.*, 2002). Atka mackerel migrate vertically in the water column during the day, whereas at night, they remain at the same depth on the bottom (Nichol and Somerton, 2002). Consequently, their patchy distribution occurs on both temporal and spatial scales.

Atka mackerel life history traits are unique among Alaskan groundfish. They have a semi-pelagic distribution over the continental shelf and upper slope during the winter, whereas during the summer, part of the population enters shallow coastal areas to spawn. Peak spawning occurs from July through October in the Aleutian Islands (McDermott and Lowe, 1997). Eggs are spawned in batches in rock crevices by females, and are fertilized and guarded by brightly colored males until hatching (Gorbunova, 1962; Zolotov, 1993). Atka mackerel spawning behavior further enhances their patchy distribution. Adult males that are actively spawning and nest-guarding are located in shallow, coastal areas. Females visit these areas to spawn, but otherwise occupy deeper offshore areas (Fritz and Lowe, 1998). Most of the population is located west of Samalga Pass and large aggregations of Atka mackerel are located at Seguam Pass, the site selected for this study (Figs 1 and 2). However, in recent years the population along the entire Aleutian chain and Gulf of Alaska has increased due to above average recruitment of 3-year-old fish in 2001 through 2003 (Lowe *et al.*, 2004). The distribution of the commercial fishery reflects the patchiness of this species and occurs in most of the local aggregations of Atka mackerel west of Samalga Pass.

METHODS

Tagging feasibility study, 1999

In August 1999, NMFS in cooperation with the School of Aquatic and Fishery Sciences, University of Washington, conducted an Atka mackerel tagging feasibility study in Seguam Pass in the Aleutian Islands, aboard the 220' factory trawler FV *Seafreeze Alaska.* The area was divided into two subareas; Area 1 was defined as inside the 20 n mi trawl exclusion zone and Area 2 was defined as outside the zone (Fig.1). In 1999, all tag releases and recoveries were made exclusively in Area 2 (Fig.1, Table 1). The purpose of this feasibility study was to develop tagging procedures to maximize numbers of fish tagged and released in good condition, and to obtain preliminary estimates of the rates of tag loss and tagging-related initial mortality.

Live tank design and setup

A live tank system with running seawater was used to hold fish at sea in preparation for tagging and release. Six live tanks (four 1000 liter and two 680 liter) were installed on the vessel and supplied with untreated seawater at a rate of 75-110 liters per minute. Water temperature and oxygen concentration were monitored at 4-6 hour intervals.

Tagging procedures in 1999

Live fish were captured from 7-17 August 1999 during short (10-30 minutes) trawl hauls from the area open to fishing (Area 2) in Seguam Pass (Fig.1). Atka mackerel were caught using a low-rise two seam hard bottom trawl with heavy duty tire gear and immediately transferred to two 680 -l tanks, with no more than 50 fish per tank. Neon-orange, individually numbered, Floy T-bar tags[1] were inserted into either side of the dorsal musculature of the fish near the anterior end of the dorsal fin with a tagging gun. Approximately 15% of the fish were doubly tagged, with the second tag inserted in the dorsal musculature on the other side of the fish. To secure the fish while tagging, fish were held in foam-lined cradles. Fish were released into a 20-cm diameter flexible fish hose supplied with running seawater that was secured at a slight angle off the side of the vessel leaving the end trailing in the water. Direct observation of the released fish suggested that the fish were able to swim away and dive as soon as they entered the water.

Tagging-related survival estimation

A study was conducted to estimate initial tagging-related survival rates and to assess the effects of handling and tagging procedures on the fish. On 18 August 1999, a 10-minute tow was made at 150-m depth using the same net described above, and less than 2000 Atka mackerel were caught in good condition. Eighty fish were randomly selected and transferred to the four large live tanks. Within each tank, 10 fish were tagged (using the same procedures as described above) and 10 were left untagged for 12 days. Fish did not feed during the study, though dried euphausiids were provided. Tanks were checked for mortalities at least every 6 hours.

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[1] Mention of brand-names does not constitute an endorsement of this product by NMFS.

Estimating population size in 1999

Tagged fish were recovered by the commercial fishery in the area open to fishing (Area 2) in Seguam Pass with the help of NMFS groundfish fishery observers (Fig. 1). The autumn Atka mackerel fishery took place from 1-7 September 1999 in the Seguam Pass area (Table 1). All vessels fishing for Atka mackerel in the Aleutian Islands carry a groundfish fishery observer. Observers estimate catch composition on a haul-by-haul basis (AFSC, 2002). All vessels caught and processed their catch on-board, including heading, gutting, and freezing fish on trays. This required each fish to be handled individually on several occasions in the factory, providing many opportunities for tag inspection. Tagged fish were given to the observer who recorded haul number, fishing location, fork length, sex, and tag number. Crew members who recovered the tagged fish were given a small reward by NMFS.

Peterson's method (Peterson, 1896) was used to estimate the size of the Atka mackerel population in the open fishing area in 1999. Haul-by-haul catches of Atka mackerel by each vessel that fished in the September Seguam Pass fishery were obtained from the fishery observer database maintained at the Alaska Fisheries Science Center (AFSC). Haul weight was converted to numbers using the average weight of Atka mackerel caught in each haul. Average weight of Atka mackerel was estimated by weighing at least 100 fish per haul (AFSC, 2002).

The 1999 Peterson estimate was adjusted for initial tagging-related mortality, tag recovery, and tag loss. Tagging-related mortality and tag reporting rates were estimated with the integrated model developed to analyze data collected in 2000 and then incorporated into the 1999 Peterson estimate. All equations and symbols are presented in the Appendix.

Full-scale tagging study, 2000

In 2000, a full-scale tagging study was conducted to estimate local abundance and movement of fish relative to the 20 n mi trawl exclusion zone in the Seguam Pass area (Fig. 2). As in 1999, the Pass was divided into Areas 1 and 2. During the 1999 study, we discovered that a relatively flat sandy region also separated Areas 1 and 2, and had low Atka mackerel abundance. This area was considered unsuitable habitat and excluded from the release locations. The release and recapture locations (Fig. 2) therefore reflect areas of preferred Atka mackerel habitat within Seguam Pass.

Fish were caught, tagged and released in each area during a tagging cruise from 22 July to 1 August 2000 aboard the chartered fishing vessel *FV Morning Star.* In Area 2 it was difficult to locate trawlable areas with dense aggregations of Atka mackerel. Therefore, all tagged fish released in Area 2 were caught in one location whereas in Area 1 fish were caught in 11 locations. Tagged fish were released as the vessel followed transect-lines within each subarea. It was assumed that releasing fish along transects would ensure random mixing within their local aggregations.

Three tag recovery events occurred (periods 1-3) in fall 2000. For the integrated model analysis, 27 July was used as the mean release date, and the midpoint of each recovery period was used as the recovery date. The first recovery event was at the fishery in Area 2 from 1-5 September 2000 (catch of 3,575 t), 37 d after the tagged fish were released. The second recovery event occurred aboard the chartered *FV Seafisher* in both Areas 1 and 2 from 23-28 September 2000, 59 d after release. The *FV Seafisher* was chartered to catch and examine 500,000 fish (approximately 500 t) for tags. The vessel was allowed to process and sell the catch, but was required to carry NMFS scientists to recover tags and fish in a predetermined and systematic way (described below). Because recovery effort in Area 1 was much smaller than in Area 2, approximately 3 times more tags were released in Area 1 than 2 to increase tag recapture probability. The third recovery event was a small commercial fishery in Area 2 from 11-13 November 2000 conducted by a single vessel 107 d after tagged fish were released.

Tagging procedures in 2000

In 2000, tagging and release procedures followed those described for the 1999 tagging study, with the exception that tow durations were kept to a minimum (10-30 minutes) and catch sizes were kept below 3 t by using an opening in the cod end to avoid injuring fish. Once fish were brought onboard they were immediately transferred to live tanks and left to settle for about 20-40 minutes. Individual fish were measured to the nearest cm (fork length) and tagged. Fish were released in a continuous transect pattern (Fig. 2). Time of release was recorded to the nearest 5 minutes and correlated to release location using a digital GPS system. For every haul, sex, determined by direct observation of the dissected gonads, and fork lengths to the nearest cm from 150 randomly selected non-tagged fish were recorded. External sexing of live fish did not seem reliable since not all male fish were in bright yellow spawning color.

Tag Recovery in 2000

For recovery events 1 and 3 (Table 1) in Area 2, tagged fish were recovered aboard commercial fishing vessels by processing crews with the help of fishery observers during their regular fishing and processing procedures (Fig.3). For recovery event 2, approximately three-fourths of the 500,000 Atka mackerel to be caught by the *FV Seafisher* were allocated to Area 1, and one-fourth to Area 2 to permit comparisons with recoveries made by the fishery (Fig. 3). To disperse recovery effort over a wide geographic area, catches were restricted to a maximum of 25 t per haul by making an opening in the side of the codend. Once the catch reached 25 t the remainder of the catch was allowed to bleed through the opening. Upon completion of a haul, the vessel was not allowed to fish within 1-n mi radius of the tow station for at least 24 hrs.

During both the commercial fishery and the chartered tag recovery on the FV *Seafisher,* Atka mackerel were commercially processed aboard the vessel. This required each fish to be handled individually on several occasions in the factory, providing many opportunities for tag inspection. Tagged fish found by the crew were given to the observer during the fishery and NMFS scientists during the chartered tag recovery who recorded haul number, fishing location, fork length, sex, and tag number and extracted otoliths when possible. Crewmembers who recovered tagged fish were given a small reward by NMFS.

Tag reporting rate in 2000

Several experiments were carried out on both the commercial vessel and the charter vessel in 2000 to estimate the proportion of tagged fish actually recovered and reported by the crew. NMFS scientists and observers tagged 10 test fish per haul and randomly seeded the catch with these fish as the catch was dumped into the fish holds. The Floy tags used for this experiment had unique numbers that identified them as test tags. Scientists and observers then recorded the number of tagged test fish reported by the processing crew. This was carried out for every haul during the NMFS charter cruise and for every haul the observers sampled on board the commercial vessels. Because the commercial fleet generally had lower reporting rates than the NMFS chartered vessel, reporting rates were estimated separately for the commercial fleet and the charter (see appendix).

Sampling of the catch in 2000

Sampling procedures aboard the commercial fishing vessels followed standardized NMFS observer sampling procedures (AFSC, 2002) and were similar to those aboard the NMFS charter vessels illustrated here. Total haul weight was determined with a Scanvaegt flow scale (model 4600) over which the entire catch passed during processing. Hauls were sampled for species composition. Three 1000-3000 kg subsamples were randomly taken during the processing of the catch in the ship's factory. Samples were sorted and weighed by species. Average weight of Atka mackerel per haul was determined by counting and weighing at least 100 fish per subsample and dividing the total weight by the number of fish sampled. Additionally, for each haul at least 150 Atka mackerel were sexed and measured for fork length.

Estimating number of Atka mackerel examined for tags in 2000

The number of Atka mackerel examined for tags was assumed to be the total number of Atka mackerel commercially caught in Area 2 plus fish captured in Areas 1 and 2 during the charter recovery cruises. The number of Atka mackerel caught per haul was calculated by dividing the haul weight of Atka mackerel by the average weight of Atka mackerel in the haul.

Determining sexed length frequencies for tag releases and recoveries in 2000

Because tagged fish were not sexed, the sex ratio for tagged fish at time of release was estimated using the sex ratios from sexed length frequency samples taken from each haul during the tagging event (Table 2). The number of male and female Atka mackerel tagged and released was estimated by multiplying the respective sex ratio with the total number of tagged fish released.

Sex ratio for all fish examined for tags at the various recovery events was calculated using sexed length frequency data that were taken for each haul during the recovery charter and for all hauls sampled by observers during the commercial fishery tag recovery. Numbers of male and female fish examined for tags were estimated by multiplying the respective sex ratio with the total number of fish examined for tags.

Sexes for tagged fish that were recovered were usually determined by observers and scientists onboard the recovery vessels and reported on tag recovery forms. However, sex could not be determined on 25 of the 104 tagged fish recovered in 2000 because the tags were discovered in the factory of a commercial vessel after the fish had been headed and gutted. Consequently, these fish were assigned a sex based on the ratio of sexed fish in the respective recovery period and area.

Tagging model in 2000

In recent years, tagging models have been developed that simulate the tagged population over time and fit it to groups of recoveries (Hilborn, 1990; Kleiber and Hampton, 1994). These models generally do not estimate population size and movement simultaneously as this will often result in overparameterization. Integrated models have been applied using additional data sources in tag release applications (Maunder, 1998). This use of auxiliary data sources allows simultaneous estimation of parameters and therefore avoids overparameterization.

The tagging model developed here (see Appendix) builds on recent advances of Hilborn (1990) and Maunder (1998). Population size and movement rates are estimated simultaneously with an integrated model using auxiliary information for tag loss, initial tag survival and reporting rate.

Model assumptions

The assumptions of this tagging model are:

1. The probabilities of catching a tagged and an untagged fish are the same (i.e., tagged fish are randomly mixed within an area)
2. Tagging does not affect catchability
3. The population is contained within the described areas (Fig. 2) therefore there is no emigration or immigration from outside Areas 1 and 2
4. Tag loss is independent of sex and occurs immediately after tagging with no systematic tag losses thereafter
5. For double-tagged fish, the probability of losing the first tag is independent of losing the second tag and both probabilities are equal
6. All mortality associated with tagging is independent of sex and occurs within 12 days of tagging (length of mortality experiment) and no systematic additional tagging mortality occurs on the tagged population
7. Natural mortality and recruitment are negligible between release and recapture events (1-3 months time interval).

Sex-specific population and movement estimates

One of the assumptions of the tagging model is that fish have the same probability of being caught at time of tagging as at time of recovery and that there is no emigration out of or immigration into the population. This implies that changes in sex ratio are due to sex-specific movement between the two areas. Sexed length frequency distributions and sex ratios at time of tagging and tag recovery were examined (Fig. 4).

Three model runs were conducted: one for both sexes combined and two for each sex separately. In the third recovery event, 5 females and one unsexed tagged fish were recovered. For the model run for both sexes, the unsexed fish was assigned the sex of male since the model would not function with zero male recoveries in one of the recovery events.

All equations are described in the Appendix. Data and model parameters are described in Table A1. The parameters of the model are estimated using an iterative minimization routine (AD Model builder, Fournier, 1998) to minimize the total negative log likelihood.

RESULTS

1999 tag release experiment

A total of 1,375 Atka mackerel were tagged and released in Area 2 in 1999 (Table 3). Of these, 219 were doubly tagged. Out of 219 doubly tagged fish, 4 were returned with both tags and 3 were returned with one tag. The tag loss rate estimate was 0.27 (CV=0.56). This estimate was much higher than the tag loss rate estimated from the 2000 experiment (l=0.05). It is not clear if the 1999 estimate accurately indicated true tag loss for this tagged group, possibly due to poor tag insertion into the fish, or if it was poorly estimated due to the small sample size (only 7 double tagged fish were recovered).

Tagging related survival estimation in 1999

Short-term survival was high with 38 of the 40 fish surviving that were tagged and 39 of the 40 control fish surviving (untagged) for 12 days after which the experiment was terminated and all fish released into the water. The fish that died during this experiment were examined for injuries and all showed a high amount of internal bruising, which was assumed to be the cause of death. The large amount of bruising was most likely caused during the capture process with a commercial trawl net. The tagging procedure itself did not seem to have a large effect on survival. A Chi square (X^2) test comparing two proportions in a binomial comparative trial (Zar, 1996) was carried out to test whether tagged fish had different survival rates than fish handled but not tagged. The test was not significant with $X^2 = 1.39$. As $X^2_{0.05,1} = 3.841$ and ($0.25 > P > 0.1$). Therefore, the data from the tag mortality study were pooled. Tagging survival rate for the 1999 study was estimated using the integrated model to be 0.9625 (Table 3).

Population size estimation for 1999

In 1999 the population size in Area 2 was estimated to be 78.9 million Atka mackerel, or approximately 79,550 t (using an average weight of 1.007 kg per fish). Tag loss rate had a great influence on our estimate of population size. If the 2000 tag loss rate is used, population size in Area 2 was estimated to be 100.1 million fish, with a biomass of 100,800 t.

Full-scale tagging study in 2000

In 2000, 6,096 Atka mackerel were tagged and released in Area 1, and 2,677 in Area 2 (Table 2, Fig. 2). In Area 1, 827 of the fish were assumed to be males and 5,269 females; in Area 2, 1,105 of the fish were males and 1,572 were females (Table 2). The proportion of double-tagged fish was 0.19 in both areas.

The number of fish examined for tags in each recovery event in 2000 is summarized in Table 2 while recoveries of tagged fish are summarized in Table 4. During recovery events 1 and 3, there was no evidence of movement from Area 1 to 2. During recovery event 2, 14 tagged fish were recovered in Area 1, 3 of which had moved from Area 2. In addition, 13 tagged fish were recovered in Area 2, 1 of which had moved from Area 1.

To estimate tag loss rate, all double-tagged recoveries were pooled from all three recovery events. Out of 1710 double-tagged fish, 19 were recovered with both tags and 2 were recovered with one tag.

Eight fishing vessels participated in the reporting rate experiment during recovery event 1. Results of the experiment are summarized in Table 5.

During the tag release cruise, no fish were found in the southwestern part of Area 1 that was close to the border of Area 2. Therefore, 557 fish were captured in Area 2 during haul 13 of the tag and release cruise and tagged and released in Area 1, in close proximity to the border (less than 2 miles). All of the six tagged fish that were recovered from haul 13 were recovered in Area 2 (Fig. 2). These were the only tagged fish that were caught in one area, but released in another. It appears that these fish may have reschooled with the population at their original capture site. Because the original capture and release sites were relatively close to each other but in different subareas, fish from haul 13 were considered to be released in Area 2 for the purposes of modeling movement and estimating biomass. This reschooling behavior may have resulted from releasing the fish in unsuitable habitat as few Atka mackerel were found over this sandy bottom separating Areas 1 and 2. All other tag releases were made in the same subareas as the original capture sites and no other reschooling behavior was apparent.

Results for both sexes combined

Population estimates for Areas 1 and 2 were 104.25 million fish (117,900 t) and 80.214 million fish (82,057 t), respectively (Table 6). There were three recovery events in Area 2 and only one in Area 1, and the total number of fish examined for tags was over 10 times greater in Area 2 than in Area 1 (Table 2). Consequently, the population in Area 2 was estimated much more precisely (95% confidence interval around the mean of 55,400 to 108,700 t) than that in Area 1 (95% CI: 27,400 to 208,400 t).

Movement probabilities and their variances for the different recovery events are summarized in Table 7. The estimated rate of movement from Area 1 to 2 ($\alpha_{1,2}$ = 0.006 after 107 days) was much smaller than from Area 2 to 1 ($\alpha_{2,1}$= 0.811 after 107 days; Table

7, Fig. 5). Confidence bounds around the small estimate of $\alpha_{1,2}$ indicate that less than 1% of the Atka mackerel population moved from the trawl exclusion zone between tag release and recovery event 3. On the other hand, $\alpha_{2,1}$ is associated with a high level of uncertainty (much like the Area 1 population estimate) because it is based on the recovery of only 3 fish that moved from Area 2 to 1 (Table 4) and a small number of fish examined for tags (Table 2). Consequently, the estimate of movement into the trawl exclusion zone is relatively uninformative.

Tagging survival and tag loss rates were estimated at 0.96 (Standard error [SE] = 0.02) and 0.05 (SE = 0.36), respectively (Table 6). The reporting rate for the commercial recovery events (Table 6) was much lower (0.73, SE = 0.02) than the reporting rate for the charter vessel (0.95, SE = 0.01). Therefore, it was necessary to estimate tag-reporting rates for the commercial fleet separately from the charter vessel. The difference in reporting rates is explained by the fact that three scientists sampled the catches during the charter cruises, whereas only one observer sampled catches taken by each commercial vessel.

Population estimates and movement rates by sex

Of the 71 (48 males and 23 females) tagged fish recovered in Area 2 in recovery event 1, none had moved from Area 1 (Table 4). During recovery event 2, 27 tagged fish were recovered, 9 of which were females and 18 males. All 3 fish that moved from Area 2 to Area 1 were males, and the one fish that moved from Area 1 to 2 was female. Of the 6 tagged fish recovered in Area 2 in recovery event 3, 5 were female and one was assigned to be a male; none had moved from Area 1.

The sex ratio of the Atka mackerel population was not the same in both areas and changed from the time of tag release in July to the recovery events in September and

November (Table 2; Fig. 4). In both areas, the proportion of males increased between July and September. When the model was run separately for each sex, total population sizes in each area (105.0 million and 75.4 million in Areas 1 and 2, respectively) were similar to those obtained for all fish combined (Table 6). However, the model estimated the population in Area 1 to be predominately female with 86.670 million females and 16.333 million males. In Area 2, the population was more evenly balanced between males and females with 46.239 million females and 29.123 million males.

Movement rates for each sex (Table 7) were different. Females had a low probability of moving between areas, while males were entirely responsible for large movement rate estimate from Area 2 to Area 1 (Fig. 5). This movement rate however was associated with large confidence bounds and is relatively uninformative.

DISCUSSION

Mark-recapture experiments have been widely used to estimate fish movement and abundance (Seber, 1982; Deriso *et al.*, 1991; Heifetz and Fujioka, 1991). The recent development of integrated models has made it possible to estimate parameters using multiple datasets, therefore incorporating all of the uncertainty into the analysis (Hilborn, 1990; Maunder, 1998). This study used an integrated model to incorporate data from a mark recapture, tag survival, and reporting rate experiment. The integrated model allows for the best use of all the information and includes uncertainty of all three experiments into the estimation of the parameters needed to measure fish movement and abundance.

Distinct and relatively closed areas of high abundance make Atka mackerel an ideal species for tag-recapture studies. The lack of a swimbladder and their hardiness enable a high tag-related survival rate if care is taken in catching, handling, and releasing them. In addition, use of observers aboard commercial fishing vessels for tag recovery was highly successful with a high reporting rate of 72%. The cooperation of fishery observers and the captains and crew of the commercial vessels in the study also provided the opportunity to measure tag reporting rates while the tag recovery was underway, something that is often difficult to obtain in mark-recapture studies.

Total population estimates for Atka mackerel in Area 2 of Seguam Pass (open to commercial fishing) from tagging studies conducted in 1999 and 2000 were similar to each other. The Area 1 (closed to the fishery) population estimate from the 2000 tagging study, while higher than the Area 2 estimate, is highly uncertain. Population estimates from the model reflect the states of the populations in each area at the time of tag release. In addition, they only reflect the population available to commercial trawl gear in the depths sampled (100-200 m).

The combined biomass in Seguam pass from Areas 1 and 2 estimated with tagging data (199,000 t) compares well to the biomass estimates from the NMFS bottom trawl survey in the Eastern Aleutians of 190,817 t and 244,043 t for 2002 and 2004, respectively (Lowe *et al.*, 2004). The trawl survey biomass estimate for 2000 in the Eastern Aleutians was unusually low which prohibited direct comparisons between tagging and bottom trawl survey data for 2000. The low 2000 estimate in the bottom survey data was likely due to the highly patchy distribution of the species in this area and associated high variances of the bottom trawl survey biomass estimate (Lowe *et al.,* 2004). Considering the inherent uncertainty and different assumptions for these assessment approaches, the biomass estimate derived from the tagging experiment falls well within the upper end of the range of estimates from the trawl survey.

The biomass estimate from the tagging experiment in Area 2 (82,000 t) was somewhat higher than an estimate derived using the Leslie depletion estimator and commercial fishery data collected in 1996 (58,000 t; 95% confidence interval of 43,000 – 73,000 t; Lowe and Fritz, 1997). These differences could have resulted from the greater area over which the tagging study estimated biomass in Area 2 and the 3-4 year difference in the timing of the estimates.

Our data suggest that from July to November 2000, less than 1% of the Atka mackerel population in the area closed to the fishery (Area 1) moved to the area open to the fishery (Area 2) in Seguam Pass. This rate is estimated relatively precisely given the large amount of recovery effort in Area 2. However, this estimate might be biased low assuming that the fish from haul 13 did not move across areas. While the model estimated the movement rate from Area 2 to Area 1 as greater than 80% for this same time period, it was associated with much higher uncertainty. The high estimate of movement was attributed almost entirely to males, while females apparently moved little between the two areas. While the high movement is estimated imprecisely, the direction is consistent with the reproductive biology of Atka mackerel. Males move to inshore areas in the summer to establish and guard nests of eggs (Zolotov, 1993), and this may have been reflected in the estimated movement rates. Additional recovery events in Area 1 may have improved the precision of movement rate and biomass estimates.

The reschooling behavior of fish from haul 13 to their local aggregation at the original capture site gives us insight into the strong habitat preferences of this species. Atka mackerel appear to be strongly associated with certain habitat and oceanographic features. These features are patchily distributed on a small scale and fish tend to seek out and return to places of preferred habitat within their local range.

The change in sex ratios observed in this study may be the result of an influx of males to the population later in the fall, as the spawning and nest-guarding season ended and males join the female population to feed in deeper waters. These data suggest that the population of Atka mackerel sampled with trawl gear and tagged in this study was not completely closed. Adult male Atka mackerel appear to be less available to commercial trawl gear during the summer than are females, a conclusion similar to that reached by Fritz and Lowe (1998) based on sexed length frequencies from fishery data. This could result in a positive bias of the population estimate because part of the tagged population would be less available to be caught during the recovery periods. Further studies are necessary to understand differences in distribution and availability of male and female Atka mackerel to trawl gear, and how these could then be used to parameterize an open population model.

The results of the tagging-recapture study conducted in 2000 suggest that the 20-n mi diameter trawl exclusion zones around Steller sea lion rookeries in the Seguam Pass area are effective in maintaining prey populations within the zone. Few fish apparently moved from inside to outside the zone during the 3+ months of the study, and the only substantial movement detected was from outside to inside. In addition, the size of the population of Atka mackerel estimated to be inside the zone is similar in size or greater than that outside.

The Atka mackerel tagging study described here is part of an ongoing effort to monitor the effectiveness of trawl exclusion zones with respect to Steller sea lion prey availability. Several key assumptions are important to consider in the overall design of the study. The assumption of random mixing is dependent on a random release effort because most of the recovery provided by the commercial fishery is not randomly distributed. When this assumption is violated, some areas might have higher probabilities of recapture than others that would bias population size low. In this study fish were captured at few locations but released along random transects. Most releases along the random transects were made close to the original capture site and within preferred grounds of Atka mackerel. However, it appeared that in one instance fish were transported away from their preferred grounds (haul 13) and released in an area where large aggregations were absent presumably because of unsuitable habitat. All tagged fish recovered from that release haul swam back and rejoined their original aggregation. All other tag releases were made within the areas of preferred grounds and the recoveries in Areas 1 and 2 show that the fish were caught relatively randomly within their preferred grounds. There did not appear to be a directional movement toward their original capture site. This indicates that Atka mackerel randomly mix within their local aggregations but will reschool to their original point of capture when transported away from preferred grounds or simply too far away from their school. To avoid the release of fish away from their original aggregation in future studies, fish should be captured at multiple random locations and released nearby.

The assumption of a closed population should also be addressed. Emigration, natural mortality and immigration parameters should be included in future models. This will likely increase uncertainty in population estimates but might not significantly change the movement rate estimates. With substantial immigration between time of tag –release and recovery, the tagged population would be diluted and population estimates would be biased high. Emigration and natural mortality are not distinguishable from each other and tend to bias population estimates low. As tagging effort continues and a time series is established, natural mortality and recruitment might be estimable in a multi-year model. Additional data sources such as catch at age might be incorporated in the development of an integrated age-based model (Maunder, 1998). Ongoing tag release efforts have been expanded farther west to other areas of high Atka mackerel abundance. Information gathered from these new study sites will improve our understanding of small scale Atka mackerel abundance and movement within the Aleutian Island system.

While prey populations inside the zone at Seguam Pass in summer and fall may be unaffected by the fishery occurring outside, little is known about the foraging behavior of Steller sea lions in this area. Andrews *et al.* (2002) reported that three short (1-2 days duration) foraging records of adult female sea lions were all in Area 1 in the summer of 1997. In March and April 2000, the at-sea locations of three of four 9-month old sea lions tagged on Seguam Island were predominately within Area 1. By contrast, the fourth tagged animal traveled over 250 km north of Seguam Island. However, the weaning status of these animals was not known, and their movements may not have been associated with foraging (Fadely *et al.*, 2005). While prey populations inside the 20 n mi trawl exclusion zone may be unaffected by the Atka mackerel fishery outside, it is unclear how prey availability to sea lions is affected if they forage outside as well. Trawl exclusion zones for the Atka mackerel fishery around all other Steller sea lion rookeries in the Aleutian Islands are only 10 n mi in diameter, and thus have only one-quarter the surface area (NMFS, 2001). This and the unique bathymetric and oceanographic features surrounding each sea lion rookery do not permit results reported here to be generalized to other Atka mackerel trawl exclusion zones in the Aleutian Islands.

The Aleutian Islands are characterized by highly dynamic currents and narrow continental shelves with steep edges. This creates a variety of microhabitats, each with its own degree of current exposure and blend of physical properties (e.g., mixing, prey abundance, temperature; Ladd *et al.*, 2005). Atka mackerel seem to be well adapted to take advantage of the most favorable microhabitats such as high relief rocky reefs with strong currents in the depth range between 100 and 200 m, resulting in their patchy distributions.

Atka mackerel is a model organism for studying the unique habitat of the Aleutian Islands. The localized pockets of extremely high abundance of Atka mackerel may be good indicators of areas with high productivity. These areas may also attract species in upper trophic levels, such as Pacific cod, Steller sea lions and northern fur seals that prey on Atka mackerel (Kajimura, 1984; Sinclair and Zeppelin, 2002). The patchy distribution of Atka mackerel may also reflect the distributions of other species that have similar feeding habits like northern rockfish and Pacific ocean perch (Logerwell *et al.*, 2005). The localized nature of highly productive areas might help to explain why Atka mackerel do not make substantial movements (more than 50 km) outside of the Seguam Pass area and may home to specific locations. Thus, individual Atka mackerel may have a relatively small home range. Once we understand the environmental and biological factors of preferred Atka mackerel microhabitats in one portion of their range (e.g., Seguam Pass), we may then understand what controls Atka mackerel distributions in other parts of the Aleutian Islands that have different bathymetric and oceanographic features. These comparisons may be very useful in understanding the differences in growth, abundance and small-scale distributions between Atka mackerel populations in the western and eastern Aleutian passes (Logerwell *et al.,* 2005), which in turn will aid in describing areas of varying productivity within the Aleutian ecosystem.

ACKNOWLEDGEMENTS

The authors would like to thank the members of the Atka mackerel fleet and the NMFS observers that assisted in collecting tagged Atka mackerel. Special thanks are due to the crew of the fishing vessels *Morning Star*, *Seafreeze Alaska* and *Seafisher*. We would like to thank Mark Tetrick who designed the live tanks used in this study and all AFSC scientists involved in the data gathering at sea, especially Peter Munro, Jerry Hoff, and Rebecca Reuter. Anne Hollowed, Libby Logerwell, Sandra Lowe, and Paul Wade helped greatly with their critical review of the manuscript. We are grateful to Grant Thompson and Jeff Laake for their advice in statistical and mathematical matters. Jim Ianelli was a tremendous source of knowledge in developing the tagging model. We would like to thank Gordon Kruse and the anonymous reviewers for their helpful review of the manuscript. Special thanks are due to Donald R. Gunderson for his guidance and support. Last, we would like to express our appreciation to Allen Macklin for his hard work as handling editor of this special issue.

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Table 1: Release and recovery events for 1999 and 2000 tag release experiments. Midpoint dates (shown in parentheses) are used to estimate days of liberty between tagging and recapture.

Year	Date (midpoint)	Event	Type	Area	Days after release
1999	August 7-17 (August 12)	Tag release	Charter	2	0
	September 1-7 (September 3)	Recovery	Fishery	2	23
2000	July 22-August 1 (July 27)	Tag release	Charter	1 and 2	0
	September 1-5 (September 3)	(1) Recovery	Fishery	2	37
	September 23-28 (September 25)	(2) Recovery	Charter	1 and 2	59
	November 11-13 (November 12)	(3) Recovery	Fishery	2	107

Table 2. Atka mackerel tagging experiment in 2000: Numbers of tagged fish released, percent of fish double tagged, and numbers of fish examined for tags for the three recovery events by sex.

Event	Area	Number of Males (% Males)	Number of Females (% Females)	Total	% double tagged
Tagged fish released					
Tag Release	1	827 (13.6%)	5269 (86.4%)	6096	0.1959
Tag Release	2	1105 (41.3%)	1572 (58.7%)	2677	0.1928
Fish examined for tags					
Recovery 1:	1	-	-	-	
Fishery	2	2,188,284 (62.3%)	1,324,357 (37.7%)	3,512,641	
Recovery 2:	1	159,356 (50.6%)	155,535 (49.4%)	314,891	
Charter	2	114,076 (73.6%)	40,927 (26.4%)	155,003	
Recovery 3:	1	-	-	-	
Fishery	2	70,639 (24.1%)	222,907 (75.9%)	293,546	

Table 3. Data and results for the 1999 tagging study.

Data	Value
T: Numbers of tagged fish released	1375
C: Numbers of fish examined for tags	5517464
E: Number of double tagged fish released	219
F: Number of double tagged fish recovered with both tags	4
G: Number of double tagged fish recovered with one tag	3
R: Numbers of tagged fish recovered	50
s: Survival rate (estimated in integrated model)	0.9625
o: Tag reporting rate (estimated in integrated model)	0.7266
l: Tag loss rate	0.27

Population estimate	
N_2: : Estimated population size in Area 2	78,996,933
B_2: Estimated biomass in Area 2 (t)	79,550

Table 4. Tag recoveries in 2000 during the three recovery events.

		Area recovered					
Recovery	Area	Males		Females		Total	
event	Released	1	2	1	2	1	2
1	1	-	0	-	0	-	0
(Fishery)	2	-	48	-	23	-	71
2	1	3	0	8	1	11	1
(Charter)	2	3	12	0	0	3	12
3	1	-	0	-	0	-	0
(Fishery)	2	-	1	-	5	-	6

Table 5. Results of the tag reporting rate experiment in 2000 aboard chartered and commercial fishing vessels.

	n_u : number of vessels	Dummy tags reported (% reported)	Dummy tags not reported (% not reported)
Commercial	1	63 (90%)	7 (10%)
Vessel	2	15 (75%)	5 (25%)
	3	55 (79%)	15 (21%)
	4	22 (73%)	8 (27%)
	5	33 (66%)	17 (34%)
	6	39 (65%)	21 (35%)
	7	23 (77%)	7 (23%)
	8	72 (65%)	38 (35%)
	Total	322 (73%)	118 (27%)
NMFS charter	1	330 (95%)	16 (5%)

Table 6. Parameter estimates for the Atka mackerel tagging study 2000 for both sexes combined (model run with total population numbers), and each males and females (each sex represents a different model run).

		Total population		Males		Females	
Description	*Symbol*	*Estimate*	*Std error*	*Estimate*	*Std error*	*Estimate*	*Std error*
Population in Area 1:	N_1	104.25	42.101	16.333	16.007	88.670	31.562
Biomass in	B_1	117,900	45,267	18,456	18,447	100,197	38,656
Population in Area 2:	N_2	80.214	9.359	29.123	4.055	46.239	8.028
Biomass in	B_2	82,057	13,311	29,793	4,328	47,303	8,446
Inst. movement rate	$\theta_{1,2}$	0.000052	0.0001	1.569E-08	1.5694E-06	0.000158	0.000161
Inst. movement rate	$\theta_{2,1}$	0.0156	0.0148	0.025738	0.050971	6.9285E-07	0.000069
Parameters estimated independent of sex							
Tag loss rate	l	0.0526	0.0362				
Tag survival rate	s	0.9625	0.0212				
Tag reporting rate for	$o_{1,2}$	0.7266	0.0214				
Tag reporting rate for	$o_{2,1}$	0.9549	0.0110				

Table 7. Movement between areas in 2000, their standard deviation and confidence intervals for the 3 recovery time periods, for both sexes combined, and males and females separately. Standard deviation and confidence intervals were calculated with the delta method.

Probability of movement at time period k	Time period (k)	Days since tagging (d_k)	Probability of movement	Std error	Lower C.I.	Upper C.I.
Both sexes combined						
$\alpha_{1,2}$	0	1	0.0001	0.0001	0	0.0002
	1	37	0.0019	0.0025	0	0.0068
	2	59	0.0031	0.0040	0	0.0109
	3	107	0.0056	0.0072	0	0.0197
$\alpha_{2,1}$	0	1	0.0154	0.0146	0	0.0441
	1	37	0.4376	0.3090	0	1.0
	2	59	0.6006	0.3500	0	1.0
	3	107	0.8107	0.3010	0.2210	1.0

Males						
$\alpha_{1,2}$	0	1	1.57E-08	1.57E-06	0	3.1E-06
	1	37	5.8E-07	5.8E-05	0	0.00011
	2	59	9.3E-07	9.26E-05	0	0.00018
	3	107	1.7E-06	0.000168	0	0.00033
$\alpha_{2,1}$	0	1	0.02541	0.04968	0	0.12277
	1	37	0.61415	0.72769	0	1
	2	59	0.78097	0.65869	0	1
	3	107	0.93633	0.34728	0.25566	1
Females						
$\alpha_{1,2}$	0	1	0.00016	0.00016	0	0.0005
	1	37	0.00583	0.00594	0	0.0175
	2	59	0.00928	0.00944	0	0.0278
	3	107	0.01677	0.01698	0	0.050
$\alpha_{2,1}$	0	1	6.9E-07	0.00007	0	0.00014
	1	37	0.00003	0.00256	0	0.00505
	2	59	0.00004	0.00409	0	0.00805
	3	107	0.00007	0.00741	0	0.01460

APPENDIX

Tagging models and related tables for the 1999 and 2000 tag experiments

The 1999 Peterson estimate was adjusted for initial tagging-related mortality, tag recovery, and tag loss. Tagging-related survival and tag reporting rates were estimated with the integrated model and then incorporated into the Peterson estimate. All symbols are defined in Table A1 unless they are mentioned in the text below.

The rate of tag loss was calculated using recoveries of double-tagged fish with a maximum likelihood estimator (Gulland, 1963):

$$l = \frac{F}{F + 2G} \tag{1}$$

where:

l = probability of single tagged fish being recovered with no tag (2)

$(1\text{-}l)$ = probability of single tagged fish being recovered with one tag (3)

l^2=probability of double-tagged fish being recovered with no tags (4)

$2(l\ (1\text{-}l))$= probability of double-tagged fish being recovered with one tag (5)

$(1\text{-}l)^2$= probability of double –tagged fish being recovered with both tags (6)

The probability that a fish does not retain at least one tag is expressed as:

$y = (1 - x)l + xl^2$ where x is the proportion of tagged fish with two tags (7)

The adjusted Peterson estimate was calculated using the unbiased Chapman estimator (Chapman, 1951):

$$N_2 = \frac{\left(T_2 s(1-y)+1\right)\left(C_2+1\right)}{\left(R_2 / \rho_2\right)+1} - 1 \tag{8}$$

R_2 = number of tagged fish released and recovered in Area 2

T_2 = number of tags released in Area 2

y = probability of not at least retaining at least one tag

ρ_2 = reporting rate in Area 2

s = instantaneous tagging survival rate (estimated in integrated model).

2000 tagging model: The integrated tagging model

Data and model parameters

Data and model parameters are defined in Table A1. A specific tag group T^r is defined as a group of fish tagged in the geographic area *r*. For this analysis there is only one time stratum for tag releases but more time strata can be added as more years of tag releases are added.

Population size and movement

This model tracks population size and movement over the time periods in which fish were recovered. Tagged fish are assumed to be released once at the beginning of the study. The tagged fish are assumed to have mixed randomly with the non-tagged population. All recovery effort is assumed to occur at the end of each time period *k*. Fish movement is modeled as a Markov process (Deriso *et al.*, 1991); the probability of being in area *i* after movement depends only on the current location *j*. Fish movement in this model is described as the daily contribution to net movement that are then expanded over the different time periods similar to Heifetz and Fujioka (1991). Because this study included only two areas, the movement matrix could be simplified and describes net movement of the population between the areas. Population size was described using the following equations:

$$N_{i,t} = N_i \qquad \text{for} \quad t = 0 \tag{9}$$

$$N_{i,t} = \sum_{j=1}^{j=A} N_{j,t-1}\, p_{j,i} \qquad \text{for } t > 0, \quad t \neq d_k + 1 \tag{10}$$

$$N_{i,t} = (1 - u_{i,k}) \sum_{j=1}^{j=A} N_{j,t-1}\, p_{j,i} \qquad \text{for } t = d_k + 1 \tag{11}$$

The daily contribution to the probability of staying in one area is modeled as:

$$p_{j,i} = e^{-\theta_{j,i}} \qquad \text{for } j = i \tag{12}$$

The daily contribution to cumulative net movement is modeled as:

$$p_{j,i} = 1 - e^{-\theta_{j,i}} \qquad \text{for } j \neq i \tag{13}$$

The harvest rate $u_{i,k}$ in area *i* at period *k* is modeled as:

$$u_{i,k} = \frac{C_{i,k}}{N_{i,t}} \qquad \text{for } t = d_k \tag{14}$$

Tagged population

It was assumed that tag loss and mortality due to handling and tagging was instantaneous and occurred shortly after tagging, based on observations during the mortality study in 1999. The probability of not at least retaining one tag (y_i) was calculated as shown for the Peterson model (equation 7). The tagged population is modeled in the following way:

$$\widehat{T}_{i,t}^{r} = T^{r}\ (1 - y_i)s \quad \text{for } t = 0 \text{ and } r = \text{i} \tag{15}$$

$$\widehat{T}_{i,t}^{r} = \sum_{j=1}^{j=A} T_{j,t-1}^{r}\ p_{j,i} \quad \text{for t} > 0 \text{ and t} \neq \text{d}_\text{k} + 1 \tag{16}$$

$$\widehat{T}_{i,t}^{r} = (1 - u_{i,k}) \sum_{j=1}^{j=A} T_{j,t-1}^{r}\ p_{j,i} \quad \text{for } t > 1 \text{ and } t = \text{d}_\text{k} + 1 \tag{17}$$

The predicted number of tags that are recovered and reported can then be expressed as:

$$\hat{R}_{i,t}^{r} = \left(\sum_{j=1}^{j=A} T_{j,t-1}^{r}\ p_{j,i} \right) u_{i,k}\ o_{i,k} \tag{18}$$

Likelihoods

Maximum likelihood was used to estimate the parameters of this model. Maximum likelihood has become the standard technique for parameter estimation in fisheries literature when using non-linear models (Maunder, 1998). Analysis for this model consists of several components that are combined in a joint likelihood and nonlinear function minimization procedure (AD Model builder, Fournier, 1998).

Tagging likelihood

Because tag recoveries can be described as rare events, the Poisson likelihood gives similar results to a multinomial likelihood (Hilborn, 1990).

The tagging likelihood (L_T) is then expressed as:

$$L_T\,(parameters \mid tag\, data) = \prod_{i=1}^{i=A} \prod_{k=1}^{k=K} \frac{e^{-\hat{R}_{i,d_k}^{r}}\ \hat{R}_{i,d_k}^{r}\ {}^{R_{i,d_k}^{r}}}{R_{i,d_k}^{r}\,!} \tag{19}$$

Tagging survival rate likelihood

The survival rate estimation was based on the 1999 experiment conducted on the FT *Seafreeze Alaska* during the tagging feasibility study. A total of 80 fish, 40 tagged and 40 untagged, were placed into four live tanks. Of the 40 tagged fish, 2 died, and of the 40 untagged fish, 1 died after 12 days. A Chi square (X^2) test comparing two proportions in a binomial comparative trial (Zar, 1996) was carried out to test whether tagged fish had different survival rates than fish handled but not tagged.

H_0: tagging did not affect fish survival and

H_a: tagging did affect survival rate.

The test was not significant with X^2 = 1.39. As $X^2_{0.05,1}$ = 3.841 and (0.25 > P > 0.1), the null hypothesis was not rejected. The data from the tag mortality study were therefore pooled with 3 fish out of 80 fish dying. Survival rate is modeled as a binomial likelihood with fish either surviving or dying from handling procedures. The initial tag survival rate likelihood (L_s) is then expressed as:

$$L_s = (parameters|data) = s^Q (1-s)^D \tag{20}$$

where:

Q = number of fish that lived in mortality experiment,

D = number of fish that died in mortality experiment.

Tag loss rate likelihood

In 2000 about 20% of all fish were doubly tagged. Tag loss rate can be estimated using recoveries from the doubly tagged fish. Tag loss rate likelihood (L_l) is then expressed as:

$$L_t(parameter \mid data) = (2l(1-l))^F \ ((1-l)(1-l))^G \, . \tag{21}$$

Tag reporting rate likelihood

The reporting rates for each commercial fishing vessel were treated as individual observations. For each commercial fishing vessel total number of test fish tagged, recovered and reported was compiled and treated as individual observations. Combined data from all fishing vessels were then used to estimate reporting rates on commercial vessels. The reporting rate for the charter vessel was calculated separately. Since the charter vessel recovered most tags in the closed area (Area 1) and fishing vessels recovered tags in the open area (Area 2) only, reporting rates by area and time stratum were calculated separately. Tag reporting rate likelihood (L_o) is then expressed as:

$$L_o(parameters \mid data) = \prod_{i=1}^{i=A} \prod_{k=1}^{k=K} \prod_{v=1}^{v=V_{i,k}} o_{i,k}{}^{H_{i,k,v}} \left(1 - o_{i,k}\right)^{(\varepsilon_{i,k,v} - H_{i,k,v})} \tag{22}$$

Estimation

The parameters of the model are estimated using an iterative minimization routine (AD Model builder, Fournier, 1998) to minimize the total negative log likelihood:

$$-\ln L_{tot} = -\ln L_T - \ln L_s - \ln L_l - \ln L_o\,. \tag{23}$$

Calculated parameters

Numbers of fish (population size) were converted to weight (biomass) using the average weight of individual Atka mackerel at the time of recovery and multiplying it by the number of fish estimated in each area. All hauls during recovery event two were used to calculate average fish weight in Area 1, and all hauls during recovery events one and three were used to calculate average fish weight in Area 2. Average fish weight (w_i) was 1.13 kg (SD = 0.16) in Area 1 and 1.02 kg (SD = 0.04) in Area 2.

The biomass estimate (t) and its variance were calculated with the following formula assuming population size N_i and average fish weight w_i are independent (Seber, 1982):

$$B_i = N_i\, w_i\, , \tag{24}$$

$$\operatorname{var}(B_i) = N_i^2 \operatorname{var}(w_i) + (w_i)^2 \operatorname{var}(N_i) - \operatorname{var}(N_i)\operatorname{var}(w_i) \tag{25}$$

The instantaneous movement rate parameters were used to calculate movement probabilities over a period of time. The time elapsed in number of days since tagging is represented by Δt , and the movement probabilities for the recovery events are then calculated by Δt being equal to d_k.

$$\alpha_{j,i,\Delta t} = 1 - e^{\Delta t\ \theta_{j,i}} \tag{26}$$

Variance was calculated using the delta method (Seber, 1982):

$$\operatorname{var}(\alpha_{j,i,\Delta t}) = \operatorname{var}(\theta_{j,i})\ (\Delta t^2 \quad e^{-2\,\Delta t\ \theta_{j,i}}) \tag{27}$$

Table A1. Data symbols and their definitions.

Symbol	Definition
Data	
T^r	Number of fish tagged and released in area *r*
$R^r_{i,k}$	Number of tags released in area *r* and recovered in area *i* at time
$C_{i,k}$	Number of fish that are examined for tags in area *i* at the end of time
$H_{i,k,v}$	Number of dummy tags reported per area *i,* time period *k,* and
$\varepsilon_{i,v,k}$	Number of dummy tags released per area *i*, observation *v,* and time
$V_{i,k}$	Number of dummy tag release observations in area *i* during time
D	Number of fish that died in mortality experiment
Q	Number of fish that lived in mortality experiment
F	Number of double tagged fish recovered with one tag
G	Number of double tagged fish recovered with both tags
x_i	Proportion of double tagged fish among single and double tagged fish
d_k	Number of days fish are susceptible to movement for time period *k*
i	Index for area
t	Time index for daily movement (days since tagging, t=0: time of
k	index for time periods
K	Number of time periods
A	Number of areas
Fundamental parameters	
N_i	Estimated initial population size at time of tagging in area *i*
$\theta_{j,i}$	Estimated instantaneous daily movement rate parameter for fish
$o_{i,k}$	Estimated tag reporting rate for time period *k*, in area *i*
s	Estimated rate of initial survival from tagging
l	Estimated tag loss rate

Table A1 (cont'd.): Data symbols and their definitions.

Symbol	Definition
Calculated parameters	
$\hat{T}_{i,t}^{r}$	Estimated size of tagged population in area *i* at time *t* that were
$N_{i,t}$	Estimated population size in area *i* at time *t*
B_i	Estimated biomass in area *i* in metric tons
w_i	Estimated average weight per fish in area *i*
$p_{j,i}$	Daily movement probability from area j to area *i*
$\alpha_{j,i,\Delta t}$	Probability of movement from area *j* to area i after time period Δt
$u_{i,k}$	Estimated harvest rate in area *i* at time period *k*
$\hat{R}_{i,t}^{r}$	Predicted number of tags released in area *r* and recovered in area *i* at
y_i	Probability that a fish tagged in area *i* loses all its tags

FIGURE CAPTIONS

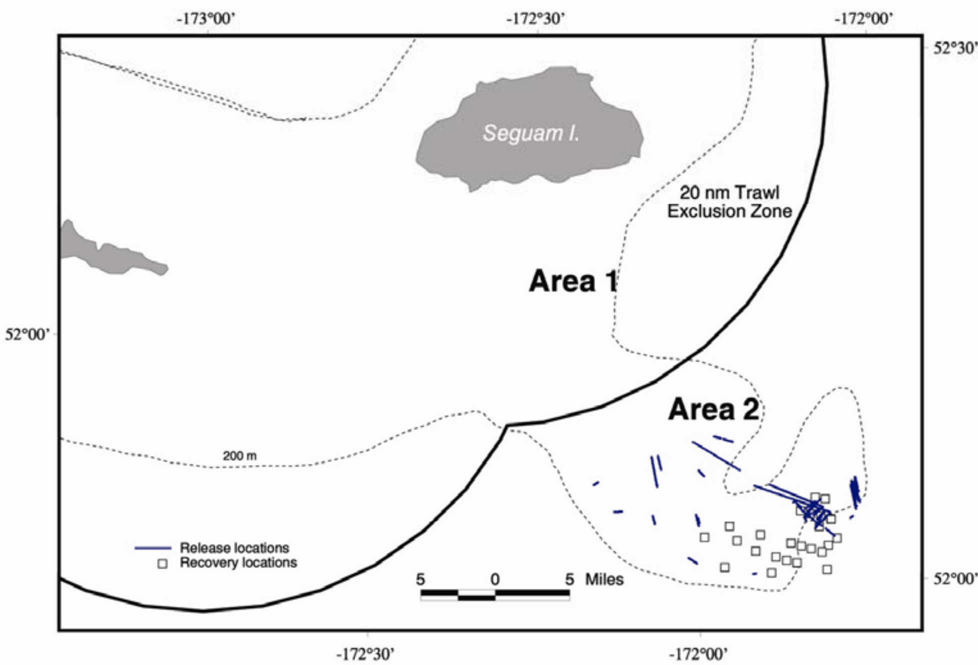
Figure 1. Tag release and recovery locations in 'Atka mackerel grounds' at Seguam Pass in 1999. Area 1 is inside the trawl exclusion zone while Area 2 is outside. Release transects are represented as straight lines and tag-recovery locations are represented as open squares.

Figure 2. Original capture and release locations of tagged fish in Seguam Pass in 2000. Capture locations of the fish to be tagged are in red, transects along which tagged fish were released into the water are shown as blue lines, except for haul 13 which is shown in green.

Figure 3. Release and recovery locations of tagged fish in Seguam Pass in 2000. Release transects are shown as a blue lines, tag recovery locations are red triangles, fish movements between tag release and recovery points are green lines, except for haul 13 which are black lines. The 20 n mi trawl exclusion zone is shown as in Fig. 1.

Figure 4. Length frequency distributions of Atka mackerel by sex during the tag release and recovery events of 2000.

Figure 5. Probability of fish movement in 2000 between Area 1 and Area 2 presented as a function of days in the water after release. Dotted lines represent the 95% confidence bounds. Probability of movement of females from area 2 to area 1 is zero, so only upper 95% confidence interval is shown in that case.



-173°00'
-172°30'
-172°00'
52°30'
Seguam I.
20 nm Trawl
Exclusion Zone
Area 1
52°00'
Area 2
200 m
Release locations
Recovery locations
5
0
5 Miles
52°00'
-172°30'
-172°00'

Fig. 1

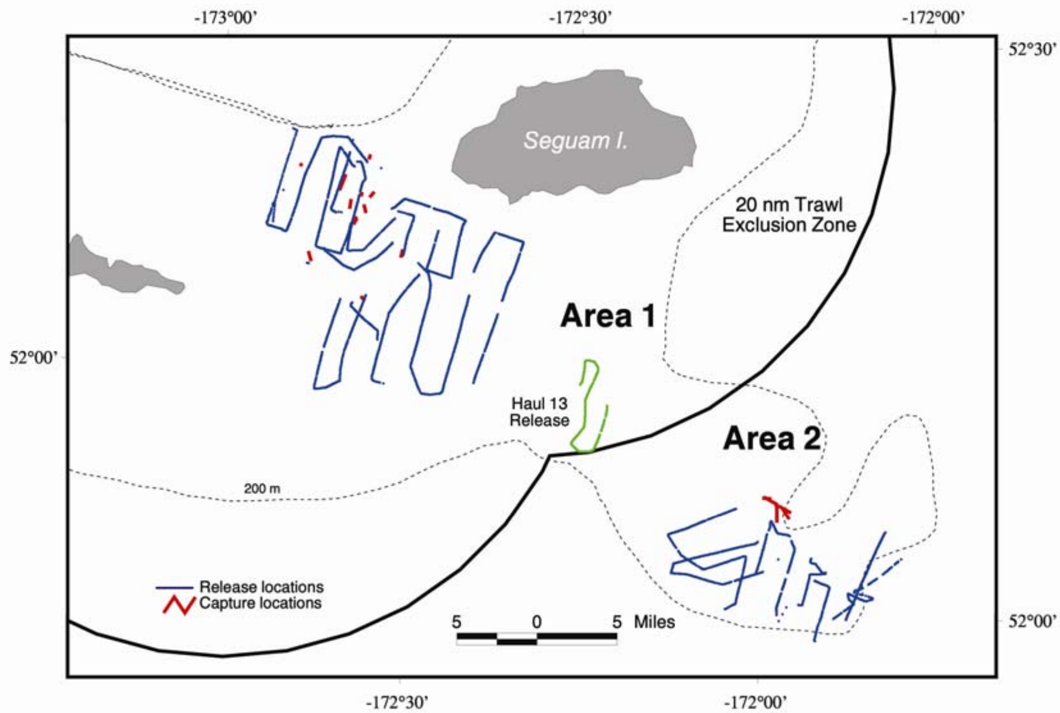

-173°00'
-172°30'
-172°00'
52°30'
Seguam I.
20 nm Trawl
Exclusion Zone
Area 1
52°00'
Haul 13
Release
Area 2
200 m
Release locations
Capture locations
5
0
5
Miles
52°00'
-172°30'
-172°00'

Fig. 2

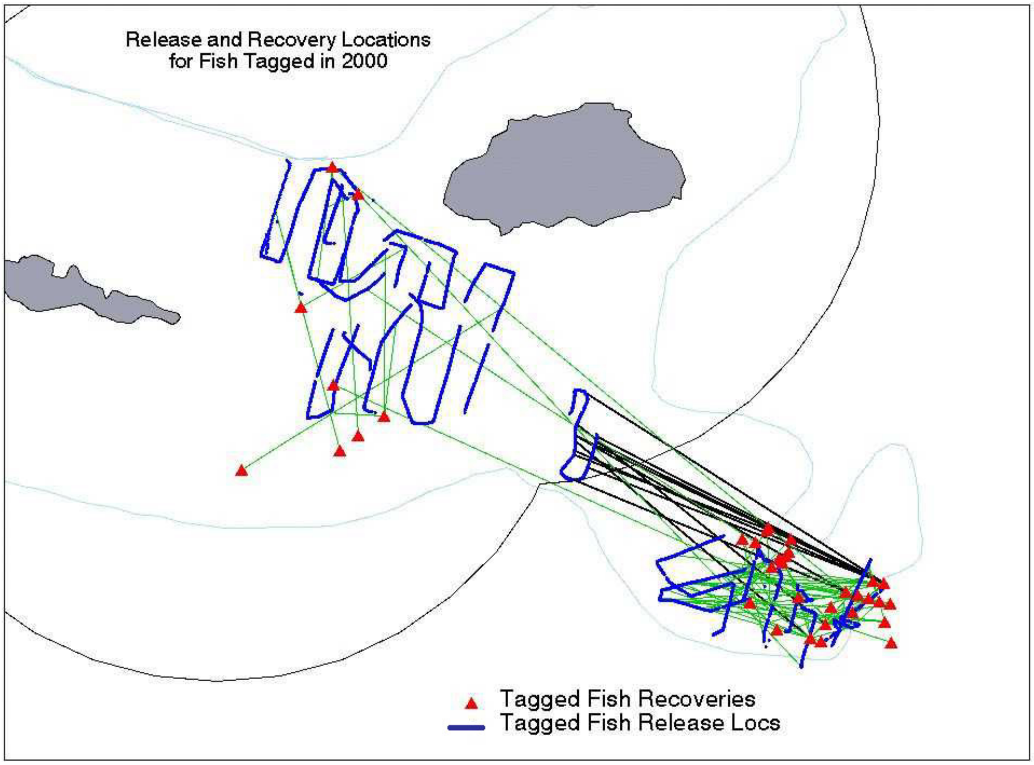

Release and Recovery Locations
for Fish Tagged in 2000
Tagged Fish Recoveries
Tagged Fish Release Locs

Fig. 3

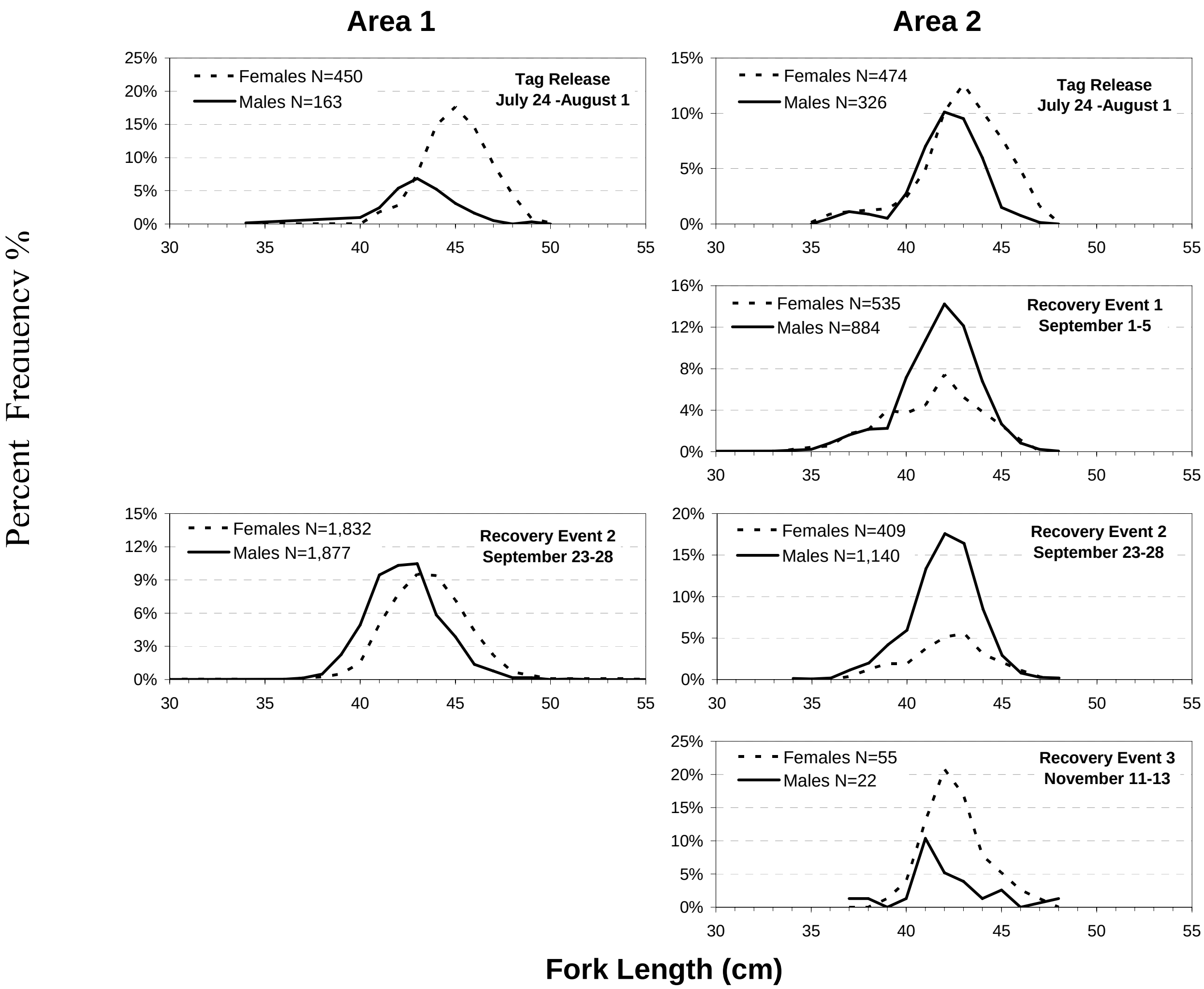

Area 1
Area 2
Females N=450
Males N=163
Tag Release
July 24 -August 1
Females N=474
Males N=326
Tag Release
July 24 -August 1
Females N=535
Males N=884
Recovery Event 1
September 1-5
Females N=1,832
Males N=1,877
Recovery Event 2
September 23-28
Females N=409
Males N=1,140
Recovery Event 2
September 23-28
Females N=55
Males N=22
Recovery Event 3
November 11-13
Percent Frequency %
Fork Length (cm)

Fig. 4

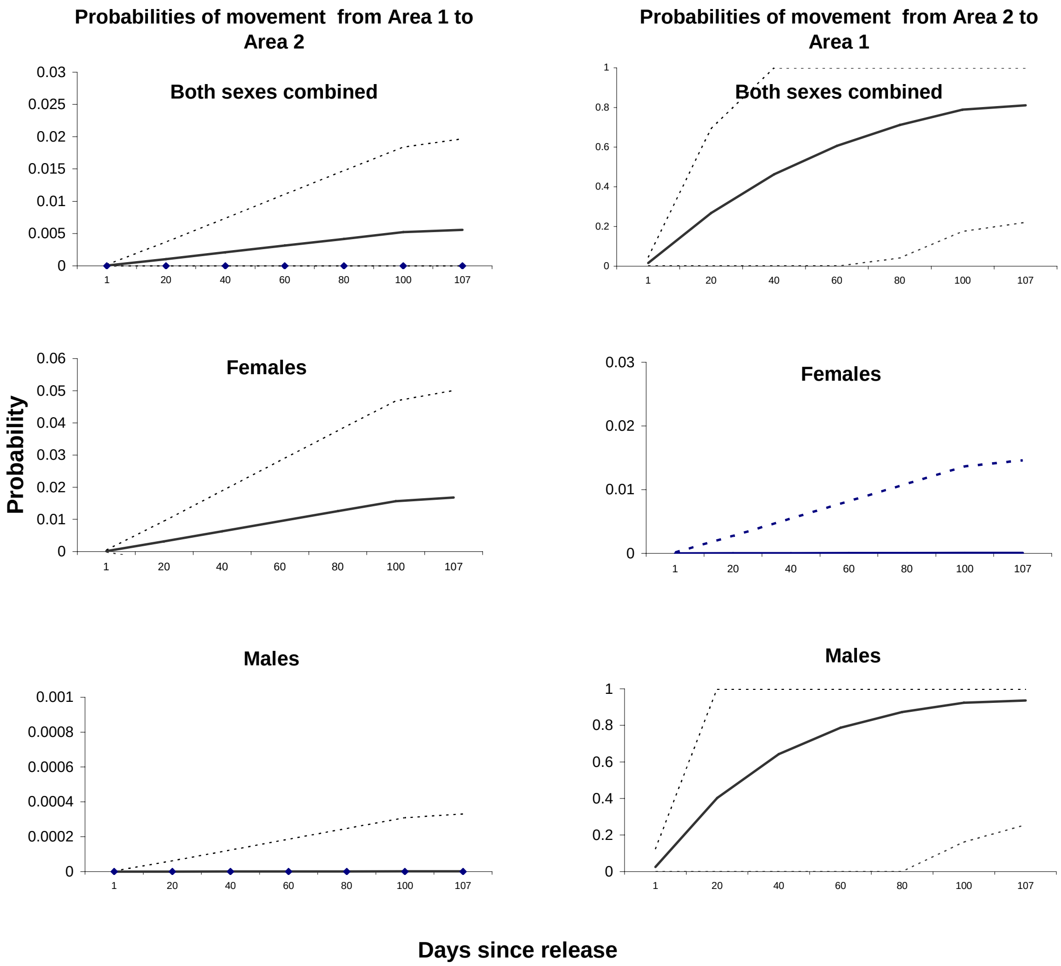

Probabilities of movement from Area 1 to Area 2
Probabilities of movement from Area 2 to Area 1
Both sexes combined
Both sexes combined
Females
Females
Males
Males
Probability
Days since release
0.03
0.025
0.02
0.015
0.01
0.005
0
1
20
40
60
80
100
107
0.06
0.05
0.04
0.03
0.02
0.01
0.001
0.0008
0.0006
0.0004
0.0002
1
0.8
0.6
0.4
0.2

Fig. 5